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Dendrochronological Reconstruction of the Historical Invasion of Balsam Woolly Adelgid, *Adelges piceae*, Feeding on Canaan Fir, *Abies balsamea* subsp. *phanerolepis* in the Central Appalachian Mountains

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ABSTRACT

During biological invasions, the initial arrival and establishment of invading populations often go unnoticed for many years yet information on early invasion dynamics is key to understanding and managing invasions. We used the presence of ring discoloration, “rotholz”, in tree cores to date historical *Adelges piceae* outbreaks and reconstruct its invasion history in 14 *Abies balsamea* subsp. *phanerolepis* stands in West Virginia. In 2018, we collected and cross-dated tree ring samples from 676 cores. We measured ring width increments and recorded the presence of rotholz in each annually dated ring. Rotholz was present in tree cores sampled from each of the 14 study sites, with the first rotholz occurrence in 1952 and widespread evidence of rotholz as early as the 1980s. Time series of rotholz frequencies indicate two synchronized waves of elevated rotholz frequencies that were observed at most sites from 1998 to 2003 and again from 2006 to 2013, coincident with observed outbreaks. Unlike patterns of growth suppression found among trees affected by defoliating insects, we observed a significant and positive relationship between rotholz frequency and standardized growth increment. This relationship is consistent with earlier observations of abnormal growth among trees infested by *A. piceae*. Our samples of rotholz frequencies suggests that rotholz may be a better indicator of past outbreaks of *A. piceae* than growth. The presence of *A. piceae* and its role in hastening decline of these rare relic tree populations would lend support to increased attention for the search for *A. piceae* biological control agents to limit damage by this insect.

Key words: non-native insect, rotholz, tree growth, tree ring, wood anatomy

INTRODUCTION

Over the last two centuries there has been a steady accumulation of non-native insect species feeding on forest trees in virtually all forest regions of the world (Brockerhoff and Liebhold 2017). While most of these insect species are innocuous, several have caused substantial impacts, including widespread mortality of host trees (Kenis et al. 2009; Fei et al. 2019). These impacts can result in substantial loss in forest market values and to non-market ecosystem services (Holmes et al. 2009; Aukema et al. 2011)

The initial arrival and establishment of invading populations often go unnoticed for years to decades (Essl et al. 2011). Many such invasions are not discovered until populations reach high densities causing noticeable damage. An example is provided by the emerald ash borer, *Agrilus*

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planipennis Fairmaire, a native to east Asia that was discovered in 2002 in Detroit, Michigan, where it was causing massive mortality of its host, *Fraxinus* spp. over a large region; subsequent dendrochronological analysis of dead trees indicated that this insect species most likely established 10-15 years before it was discovered (Siegert et al. 2014). Another example is the hemlock woolly adelgid, *Adelges tsugae* Annand, which is also native to east Asia and was discovered by entomologists sampling a garden in Richmond, Virginia, in 1954, although historical records indicate that it may have been introduced in 1911 with hemlock trees planted in that garden (Havill and Montgomery 2008). Such historical reconstruction of invasions is particularly difficult for small insects since they are cryptic and often go noticed. Understanding the pacing and trajectory of past invasions may help inform efforts to identify and slow the rate of insect invasions in the future.

Here we investigate the timing of the introduction of the balsam woolly adelgid, *Adelges piceae* (Ratzeburg), to the central Appalachian Mountains. This species is native to Europe but it exists there at sparse levels, causing little damage. Populations in North America feed exclusively on *Abies* spp. and often reach high levels that cause crown dieback or tree mortality (Hain 1988). The first observation of the species in North America was in 1908 in Brunswick, Maine, where it was believed to have been introduced with host *Abies* imported from Europe (Kotinsky 1916). Populations have subsequently spread through the Maritime provinces and the northeastern United States. Another introduction was discovered in California in 1928 (Annand 1928). Several secondary invasions in North America followed; these included its discovery in North Carolina in 1955 where it was found feeding on Frasier fir, *Abies fraseri* (Pursh) Poir and causing considerable tree mortality (Amman 1962).

Despite these early observations in surrounding regions, the first discovery of *Adelges piceae* in the central Appalachians was not made until 1992. U.S. Forest Service entomologist Robert Acciavatti noticed damage in a Canaan fir, *Abies balsamea* subsp. *phanerolepis* (Fernald) A.E. Murray, seed orchard located in the Canaan Valley of Tucker County, West Virginia (Robert Acciavatti, personal communication). While balsam fir, *A. balsamea*, is a widespread species through much of eastern Canada and the eastern and northcentral United States, the *phanerolepis* subspecies has a limited distribution consisting of only a few small, isolated stands in Tucker, Randolph, and Pocahontas counties of West Virginia. These stands are considered relic populations of *A. balsamea* created as the species shifted northward following the last glaciation (Allard and Leonard 1952; Potter et al. 2010). Between 1993 and 1998 the West Virginia Deptartment of Agriculture conducted surveys for the presence of *A. piceae*. A survey in 1993 found it present in 11 out of 26 Canaan fir stands in Tucker, Randolph and Pocahontas counties. The 1994 survey detected *A. piceae* in 15 out of 26 Canaan fir stands. By 1998, surveys reported it present at all sites and noted appreciable tree mortality. However, the small size of *A. piceae* means that this insect is easy to overlook so it is possible that the insect was present in stands earlier.

Interactions between the insect and its host tree provide an opportunity to reconstruct past outbreaks of the insect using tree ring methods. *Adelges piceae* feeds on tree sap, either by piercing twigs or on stems. During feeding, they inject saliva containing auxin-like compounds and enzymes (Balch et al. 1964; Hain et al. 1991) into plants. In stems, this causes abnormal growth (swollen tissue) around feeding sites, termed “gouting” (Balch 1952; Hain 1988). Adelgids feeding on stems also cause abnormalities in tree tissue; previous studies show a red staining of xylem (termed “rotholz”) resembling compression wood that is evident adjacent to where stylets of feeding A. piceae pierce the bark (Balch, 1952; Hain, 1988). Here, we used the presence of rotholz in tree cores to date historical A. piceae outbreaks and reconstruct its invasion history in the central Appalachian region.

MATERIALS AND METHODS

Study Sites

We sampled 14 *Abies balsamea* stands in the highlands of West Virginia in 2018 (Table 1, Figure 1). Currently much of this region is managed by the U.S. Forest Service and U.S. Fish and Wildlife

Table 1. Sample site summary including three letter site ID, location, elevation, samples collected, and duration of the chronologies (ABBA is *Abies balsamea*; PCRU is *Picea rubens*).

Site ID	Latitude	Longitude	Elevation (m)	Stand Origin	Interseries *R*		No. Cores		Chronology Length	
					ABBA	PCRU	ABBA	PCRU	ABBA	PCRU
BDR	38.83829	-79.6430	902	planted	0.396	0.549	31	19	1966–2016	1911–2017
BFT	39.11899	-79.4934	945	planted	0.487	0.547	48	26	1943–2017	1829–2017
BRS	38.60044	-79.8516	1145	natural	0.449	0.407	24	3	1946–2016	1925–2016
COR	39.08327	-79.4228	963	natural	0.425	0.443	58	10	1945–2016	1930–2017
DOL	39.01541	-79.4619	990	natural	0.344	0.504	16	20	1944–2016	1922–2017
DRT	39.01961	-79.3796	1125	natural	0.359	0.443	60	26	1965–2016	1749–2017
FRE	39.02550	-79.4278	987	natural	0.479	0.534	59	9	1961–2017	1941–2017
MAL	39.08625	-79.4372	980	natural	0.499	0.438	58	11	1949–2017	1936–2017
MSH	38.20188	-80.2340	1254	planted	0.557	0.549	59	20	1973–2017	1975–2017
MVT	39.11692	-79.3583	964	natural	0.430	0.514	29	8	1932–2016	1941–2016
RMR	39.06417	-79.4481	993	natural	0.450	0.660	59	20	1964–2016	1968–2017
SEW	39.03521	-79.4622	987	planted	0.339	0.472	60	21	1952–2016	1922–2017
UPT	39.17146	-79.3529	972	natural	0.413	0.465	55	22	1944–2017	1920–2017
VFD	39.05124	-79.4580	989	natural	0.302	0.484	60	28	1973–2016	1924–2016

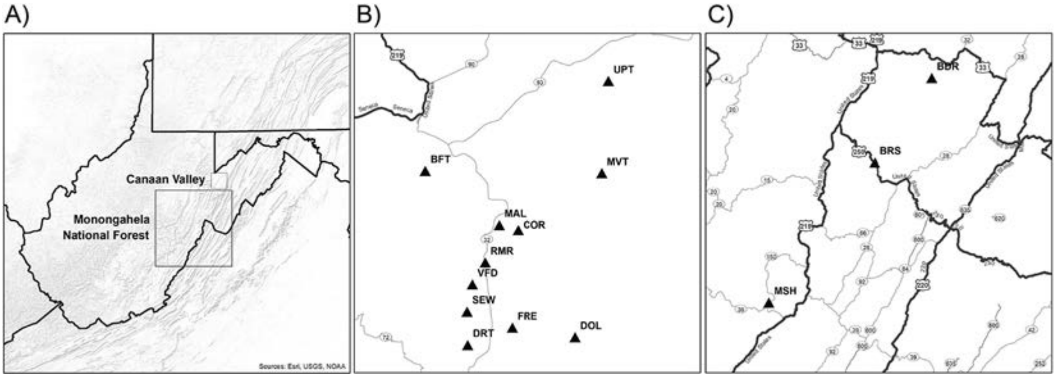

Figure 1. Location of study sites (see Table 1 for site descriptions). **A.** reference map. **B.** sites in the Canaan Valley. **C.** location of sites in the Monongahela National Forest.

Service. Prior to European settlement, most of this area was dominated by extensive spruce-fir ecosystems (Allard and Leonard 1952). The region was extensively logged in the late 19th century (Clarkson 1964), followed by repeated wildfires and grazing, resulting in elimination of most spruce-fir forests. Stands dominated by red spruce (*Picea rubens* Sarg.) remain in many of the highest elevations but fir only occurs in a few isolated localities, typically wet high-elevation sites. In addition to red spruce and balsam fir, other common species present in spruce-fir stands are yellow birch (*Betula alleghaniensis* Britton), black cherry (*Prunus serotina* Schur) and black ash (*Acer negundo* L.) (Fortney and Rentch 2003; Bartgis et al. 2015). A few stands containing balsam fir were planted during U.S. Forest Service reforestation efforts in the mid-20th century.

Field and Laboratory Method

At each site, we extracted two increment cores at breast height (1.37 m) from up to 30 live *Abies balsamea* trees >10 cm DBH. Trees were selected to represent varying crown health and diameter. We also sampled two cores from at least 10 mature red spruce trees from each site (except for stands where spruce was absent) to compare radial growth of balsam fir with a non-host species. We mounted the increment cores on wooden blocks and sanded them with progressively finer grit sandpaper (220, 400, and 600 grit) to reveal cellular structure under magnification (Stokes and Smiley 1996). Mounted samples were then cross-dated using skeleton plots to assign calendar dates to each ring. We measured the dated annual rings using a sliding stage to 0.001 mm precision and then confirmed cross-dating using the statistical program COFECHA (Holmes 1983). Once all samples were cross-dated and measured, we recorded the presence or absence of rotholz by year in each sample (Balch 1952; Hollingsworth and Hain 1992). Rotholz rings were identified as abnormally dark rings with high proportions of latewood and altered cellular structure (Figure 2). Rotholz rings were differentiated from compression wood by observing swollen, rounded cells surrounded by intercellular space.

Analytical Methods

To remove size-related radial growth trends, we standardized and detrended tree ring measurement series using a modified negative exponential curve in the dplR package for R (Bunn 2008; R Core Team 2021). We then created mean growth chronologies for each species at each site using Tukey's biweight robust mean and bootstrapped 95% confidence limits around the chronologies using the R package boot (Canty and Ripley 2021). *Abies balsamea* and *P. rubra* growing in the same ecological settings share climate sensitivities (Leef 2019) allowing for the potential detection of *Adelges piceae* impacts by comparing growth of the host (*A. balsamea*) with that of a non-host (*Picea rubra*) species. However, due to the varying effects of *A. piceae* on radial growth of individual *A. balsamea* trees, we did not employ methods developed for detecting impacts of defoliating insects

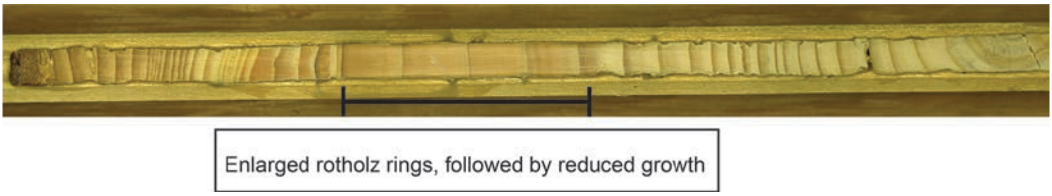

Figure 2. Rapid growth and red staining of xylem ("rotholz") along radial growth core of *A. piceae* feeding site.

using host and non-host species (Guiterman et al. 2020). Instead, we compared trends in mean chronologies at sites where we sampled sufficient cores (>=20) from each species.

Spatial synchrony in the annual proportion of rings with rotholz at each site from 1950 to 2017 was quantified using the Sncf function in the R library NCF (Bjørnstad 2016). Prior to analysis, data from years with less than five cores per site were removed.

RESULTS

Red staining of xylem was observed in a large fraction of sample cores and was interpreted as rotholz. Rotholz was present in tree cores sampled from each of the 14 study sites (Figures 3 and 4). The oldest growth ring with rotholz was from 1952 but this consisted of only one core at UPT out of 32 total samples from seven sites. By 1980 sample depth was sufficient (>357 fir cores from 14 sites) and overall, rotholz was present in 3% of samples (Figure 5). However, overall rotholz frequency did not exceed 10% until 1992. During the period 1992–2016 rotholz frequency generally exceeded 10% and there were two distinct peaks in rotholz frequency in 2000 and a second peak in 2010. This same approximate pattern of two distinct peaks in rotholz frequency between 2000 to 2016 is evident in time series from most individual stands (Figures 3 and 4). Regional synchrony in annual rotholz frequency among all sites was estimated as 0.36; the 2.5 and 97.5 percentiles of synchrony between sites were estimated as 0.19 and 0.54 indicating significant spatial synchrony in rotholz dynamics across all sites.

There was a significant association of increased growth increment associated with episodes of high rotholz incidence (Figure 6). For example, at the BDR sites, there was a period of increased standardized growth increment from 2009–2015 which generally coincided with a period during which rotholz frequencies exceeded 20% (Figure 3). Similarly, at the FRE site, growth increment was generally elevated from 2002–2015 and this coincided with a period of elevated rotholz frequency exceeding 20%. Similar patterns are seen at some of the sites where both spruce and fir were growing together (Figure 4). Standardized fir increment exceeded the 95% confidence limits of standardized spruce increment from ~1996–2000 at BFT, DRT and SEW and again from 2007–2013 at RMR, SEW and UPT. This pattern coincided with periods of exceptionally high rotholz frequencies during similar periods.

DISCUSSION

In this study, we lacked independent data on *Adelges piceae* abundance in the study region so inference about outbreaks is derived from time series of rotholz frequencies. Previous dendrochronological studies documented that rotholz production is a characteristic damage produced by *A. piceae* feeding on tree stems (Balch 1952; Hain et al. 1991; Hollingsworth and Hain 1992). Time series of rotholz frequencies across the 14 study sites indicate two synchronized waves of elevated rotholz frequencies that were observed at most sites from 1998 to 2003 and again from 2006 to 2013 (Figures 3, 4, and 5). We interpret these two peaks of rotholz incidence as the result of two distinct *A. piceae* outbreaks synchronized across the region. The first of these outbreaks roughly coincides with the initial detection of *A. piceae* life stages at a single site in the region in 1992 followed by detection of this insect species at more sites during successive surveys. A survey in 1998

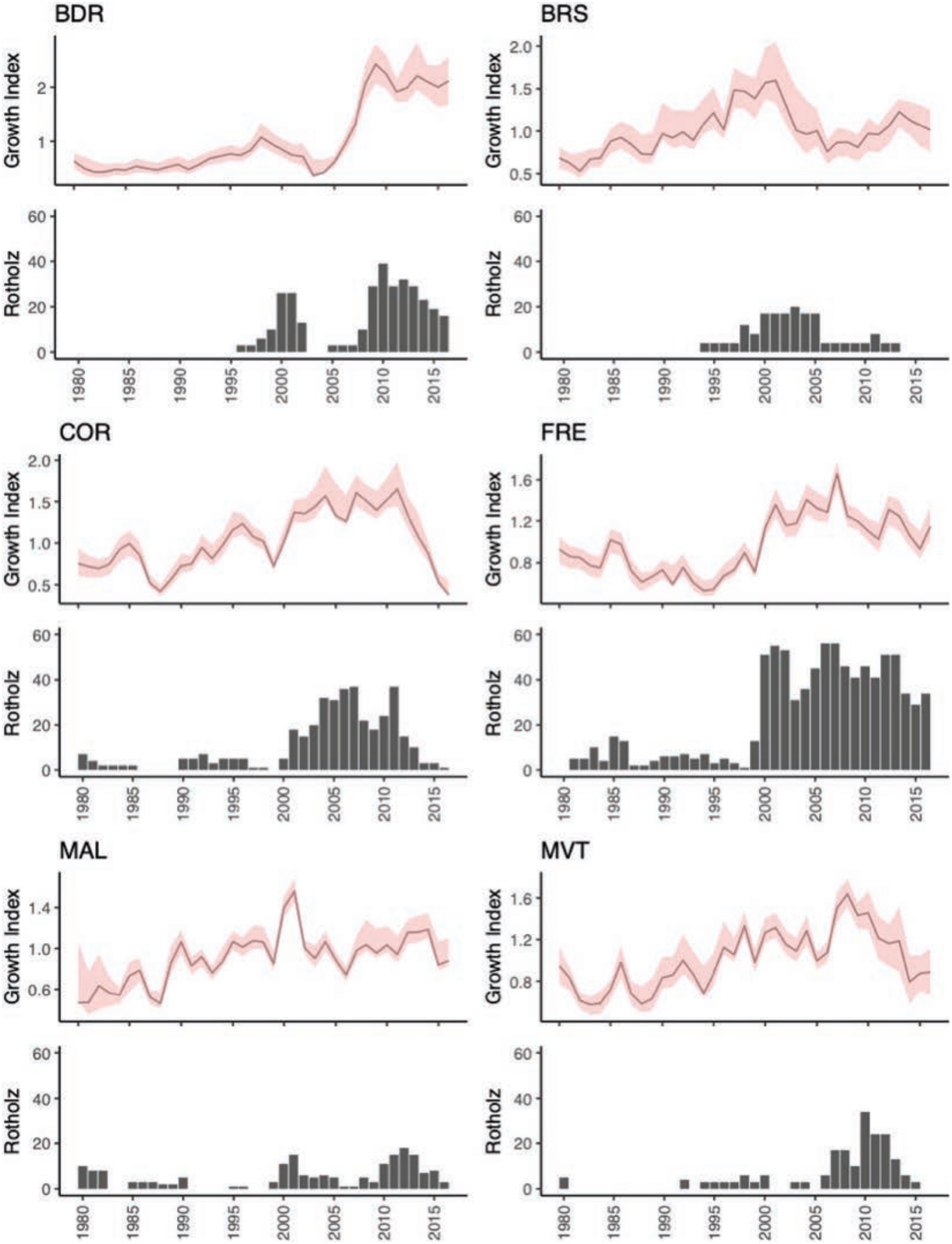

Figure 3. Mean standardized radial fir growth increment ("Growth Index") chronologies (lines) and their bootstrapped 95% confidence intervals (shading), along annual rotholz frequencies, at 6 sites (3-letter site IDs are noted in upper left in all caps, refer to table 1 for details) lacking spruce.

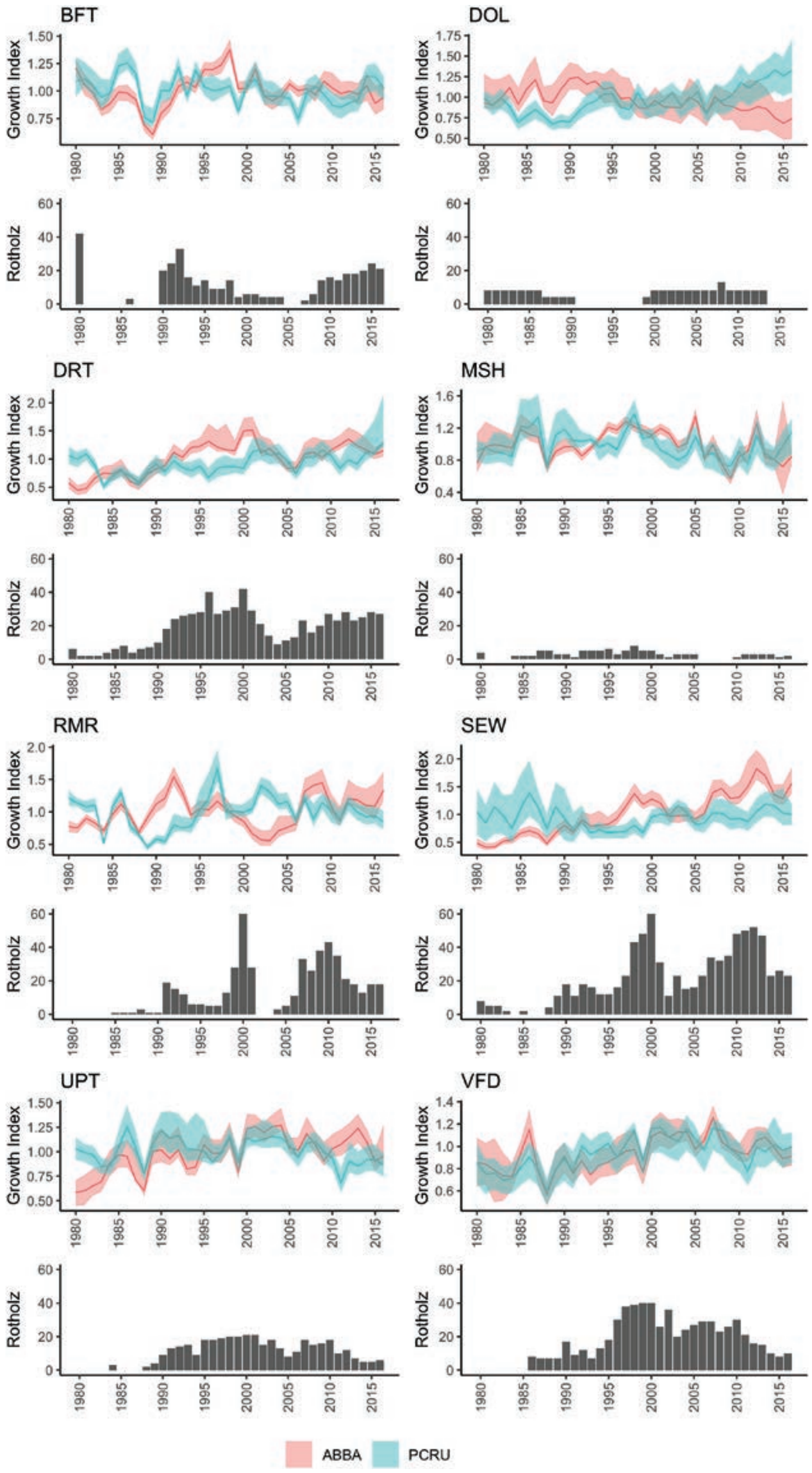

Figure 4. Mean standardized radial fir (red) and spruce (blue) growth increment ("Growth Index") chronologies (lines) and their bootstrapped 95% confidence intervals (shading) with annual rotholz frequency (black bars) for sites with sufficient data for spruce and fir (3-letter site IDs are noted in upper left in all caps, refer to table 1 for details).

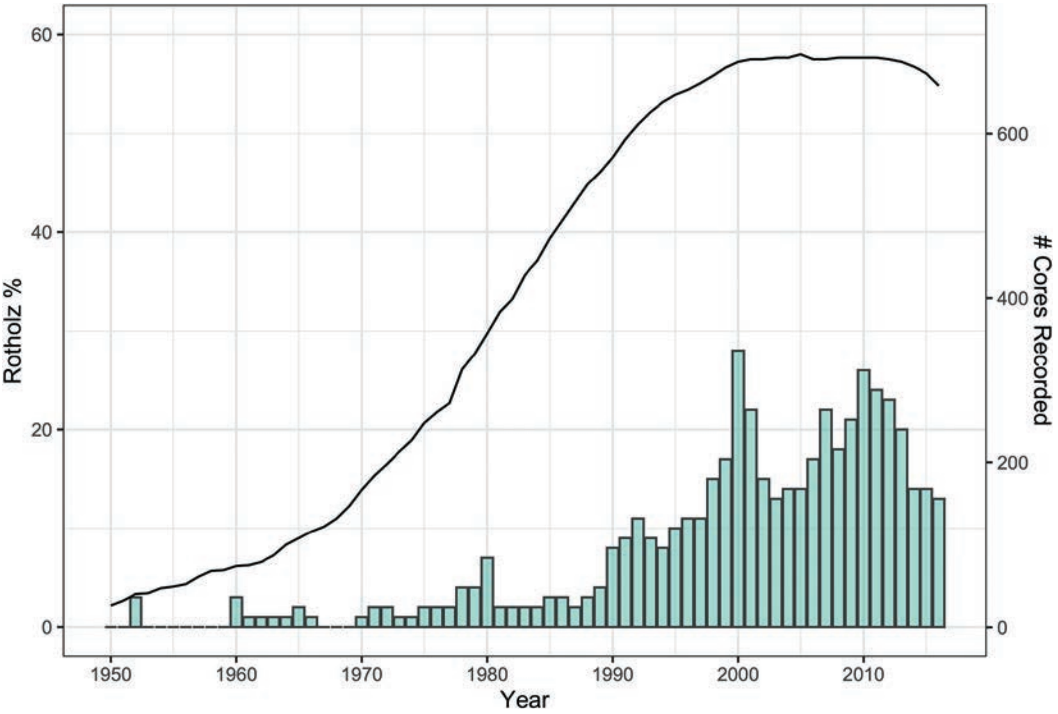

Figure 5. Time series of rotholz incidence (bars) for all study sites combined and the total number of cores recording that year (black line).

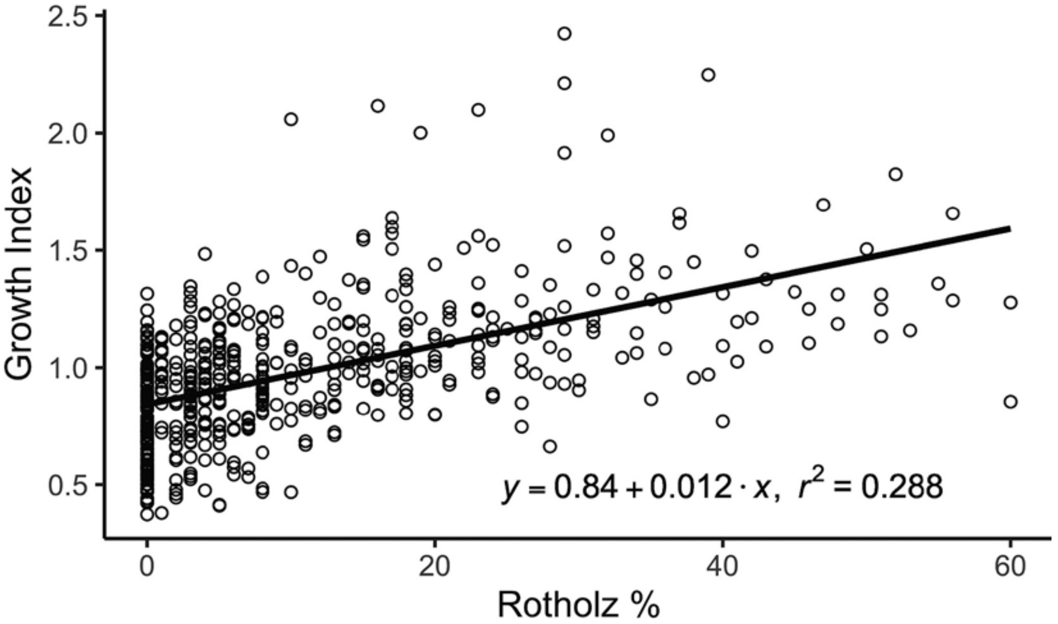

Figure 6. Relationship between percent of trees with rotholz and mean standardized *A. balsamea* growth increment ("Growth Index") (each point represents data from a single site each year).

recorded considerable tree mortality resulting from *A. piceae* outbreak populations (Hutchinson unpublished).

Though the first ring with rotholz detected in our tree cores was from 1952, sampling depth was low as fewer than 10 trees had inner ring dates prior to 1970 (Figure 5) and this may have been an anomalous observation. While Balch (1952) found that the presence of only a single feeding adelgid can result in rotholz, Hollingsworth and Hain (1992) found that occasionally rotholz may be present in *Abies fraseri* when *Adelges piceae* is absent. Thus, the presence of rothoz in a single tree in 1952 does not necessarily indicate that *A. piceae* was present in West Virginia in that year. Sampling depth did not become substantial (>20 cores) until 1973. We note, however, that rotholz was detected at low levels from ~1970–1989. Even though *A. piceae* was not discovered until 1992, it is quite possible that this insect invaded the region much earlier and was responsible for the rotholz seen in rings from 1970–1989. Adelgids are small, inconspicuous insects that would be unlikely to be noticed except when they reach outbreak levels. Indeed, discovery of the congener *A. tsugae* was made about 40 years after it was likely initially introduced and established (Havill and Montgomery 2008). *Abies piceae* was observed in North Carolina fir as early as 1955 (Amman 1962). Thus, we suspect that *A. piceae* was likely established in this region by 1970 or earlier but it took several years before reaching outbreak levels in the 1990s.

Many foliage-feeding insects cause a reduction in tree growth increment that can be used as a signature for their outbreaks in dendrochronological analyses (e.g., Swetnam and Lynch 1993; Rentch et al. 2009). However, our results suggest the opposite, that during *Adeges piceae* outbreaks, host fir trees exhibit abnormally high radial growth increment. We found a significant positive relationship between rotholz frequency and standardized growth increment (Figure 6). Observations by Balch (1952) describe increased radial growth on stems that are heavily infested with *A. piceae*. He concluded that saliva injected into trees resulted in abnormally high growth much like feeding on twigs causes abnormally swollen growth or “gouting”. Sexpurae of many adelgid species induce abnormal growth in hosts to produce galls, though this is not the case for *A. piceae* in North America due to the lack of suitable hosts. Subsequent work has shown that the abnormal enlargement of cell walls which produces rotholz limits transport in the sapwood and phloem, ultimately leading to tree decline and death (Hain 1988; Hain et al. 1991). Balch (1952) observed that while growth increment initially increased following the build-up of *A. piceae* populations, some trees’ growth would decline for a few years before tree death. Thus, even though the positive relationship between rotholz frequency and growth increment seen in Figure 6 reflects the reaction of abnormal growth to adelgid feeding, Balch’s (1954) observation of declining growth following extended outbreaks may explain why this relationship is not stronger. Further, because we only sampled living trees, we may have missed patterns of reduced growth and mortality among heavily infested trees.

Relic populations of *Abies balsamea* subsp. *phanerolepis* subspecies are extremely limited in extent, present in only a few small, isolated stands in West Virginia. Given that these stands lie on the southern range of *A. balsamea*, and are restricted to isolated high elevation areas, they likely are influenced by cold climatic conditions. Warming conditions following the last glaciation have likely caused *A. balsamea* to shift its range northward (Bazukis and Hansen 1965) and these stands may be limited in their ability to tolerate warm temperatures, a phenomenon likely exacerbated by recent warming. Limited survey information indicates that invasion of these stands by *Adeges piceae* has contributed to increases in tree mortality (Cherefko et al. 2015). However, our samples of rotholz frequencies in extant living trees suggests that past outbreaks of A. piceae may have gone unnoticed. Additional data on long-term mortality of *A. balsamea* subsp. *phanerolepis* are needed. The role of *A. piceae* in hastening decline of these relic tree populations would lend support to increased attention for the search for *A. piceae* biological control agents to limit damage by this insect. While earlier searches for biological control agents targeting *A. piceae* have been largely unsuccessful, new evidence suggests that predaceous flies (Diptera: Chamaemyiidae) may hold promise for control of closely related adelgids (Ravn et al. 2012) and future exploration may identify species suitable for control of *A. piceae*. The presence of rotholz in tree cores may provide an early indication of infestation not observed in tree growth or when insect populations are low.

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